The Abundance of the Hawaiian Trees and the Number of Their Associated Insect Species

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In a recent paper on the number of insect species associated with British trees (Southwood, 1960), the author suggested that the reason why some trees had more associated insect species than others was not entirely a matter of the biochemistry of the plant, but to a large extent a reflection of the abundance of the tree in recent geological history. When allowance is made for this effect of the host-tree's abundance on the number of insect species, then certain trees can be shown to have more or fewer insect species than might be expected from a consideration of abundance alone. It is these trees whose structural and biochemical properties are probably peculiar in some way and therefore would warrant a further investigation.

The British flora and fauna are largely just a sample of that of the Palaearctic region, and although Southwood (1960) was able to show in a comparison of Britain with Cyprus and Russia that the number of associated insect species showed a direct correlation with the abundance patterns of the trees in each country, it is not clear whether this relationship (of abundance with insect species) is due mainly to an evolutionary process or to the chances of an immigrant species finding its correct host plant or both. A large number of both the tree and insect species of Hawaii are endemic and, therefore, if a similar relationship could be shown to exist in these islands, this would indicate that such relationship is evolutionary and not just a dispersal effect, confined to an area (e.g. Britain) on the periphery of a faunal and floral region.

Swezey (1954) has provided a comprehensive list of the insect species associated with various trees and plants in the Hawaiian forest. This is based on over 40 years collecting by Dr. Swezey and on observations by other workers. He points out that future studies will add to the list, but it seems unlikely that these omissions of undescribed species are biased in the direction of any particular abundance group of trees. It might be suggested that a more serious source of bias would be the difficulty of making many collections from the rarer trees. Against this should be set the tendency to collect from a rare tree whenever encountered.

The total number of insect species attached to each tree and the number of species specific to it have been taken from Swezey (1954) and are given in table 1.

A measure of the relative abundance of the different Hawaiian trees—before the large scale disturbance by man in this century—has been taken from the descriptions by Rock (1913) and in doubtful cases checked against Hillebrand (1888). Four groups are recognised: the first contains those species described as "local" or "rare", sometimes occurring in only one locality; the second those said to be "not uncommon" or "rather common" in many areas or "common" in a few more restricted localities; the third, widespread species which are "common" or "most common"; and the fourth two trees only, *Acacia koa* and *Metro-*

TABLE 1. Hawaiian trees grouped according to abundance (pre 20th century) with the numbers of associated insect species (based on Swezey, 1954). (x=significant at 5% level, xx=significant at 1% level, xxx=significant at 0.1% level).

TREE	NUMBER OF ASSOCIATED INSECT SPECIES		
	UNIQUE ON THIS TREE ONLY	OTHERS	TOTAL
GROUP 1 "LOCAL" and "RARE"			
Claoxylon sandwicense	0	7	7
Drypetes phyllanthoides	1	5	6
Mezoneurum kauaiense	1	3	4
Pteralyxia macrocarpa	1	7	8
Pterotropia kauaiensis	5	5	10
Rauwolfia sandwicensis	1	0	1
Reynoldsia sandwicensis	1	0	1
Xylosoma hawaiiensis	4	4	8
Mean	1.8	3.9	5.6
"t" for comparison with mean of group 2	1.94	1.81	3.45 xx
GROUP 2 "NOT UNCOMMON" and "RATHER COMMON"			
Acacia koaia	0	24	24
Alphitonia excelsa	0	12	12
Antidesma platyphyllum	5	11	16
Bobea elatior	7	14	21
Charpentiera spp.	5	8	13
Dracaena aurea	4	9	13
Erythrina sandwicensis	1	10	11
Myoporum sandwicense	6	19	25
Nothocestrum spp.	2	0	2
Pandanus odoratissimus	6	16	22
Plectronia odorata	2	3	5
Pritchardia spp.	10	12	22
Sapindus spp.	0	4	4
Syzygium sandwicense	4	13	17
Tetraplasandra spp.	5	15	20
Wilkstroemia	7	21	28
Zanthoxylum spp.	2	11	13
Mean	3.9	11.9	15.8
"t" for comparison with mean of group 3	2.99 xx	2.84 xx	3.56 xxx

TABLE 1—(Continued)

TREE	NUMBER OF ASSOCIATED INSECT SPECIES		
	UNIQUE ON THIS TREE ONLY	OTHERS	TOTAL
GROUP 3 "COMMON" and "WIDELY DISTRIBUTED"			
Aleurites moluccana	1	16	17
Broussaisia arguta	10	16	26
Cheirodendron spp.	9	12	21
Coprosoma spp.	13	47	60
Dodonaea viscosa	7	14	21
Dubautia spp.	14	31	45
Elaeocarpus bifidus	5	23	28
Euphorbia spp.	25	9	36
Gouldia spp.	9	35	44
Hibiscus spp.	8	20	28
Ilex anomala	1	10	11
Maba spp.	4	12	16
Myrsine spp.	15	26	41
Osmanthus sandwicensis	3	12	15
Pelea spp.	27	10	37
Perrottetia spp.	3	15	18
Pipturus spp.	39	75	114
Pisonia umbellifera	7	20	27
Scaevola spp.	4	36	40
Sophora chrysophylla	13	31	44
Straussia spp.	14	29	43
Styphelia tameiameia	10	22	32
Urera sandvicensis	6	9	15
Mean	10.7	23.0	33.9
"t" for comparison with mean of group 4	2.11 x	3.00 xx	4.15 xxx
GROUP 4 "VERY ABUNDANT"			
Acacia koa	41	110	151
Metrosideros polymorpha	40	56	96
Mean	40.5	83.0	123.5

sideros collina polymorpha, which appear to have been the dominants on the islands. When there is a large genus of allied trees (e.g. *Myrsine*) or a few tree species allied to numerous herbaceous ones (e.g. *Euphorbia*) these are placed in a higher abundance group than that appropriate for the individual species. This is because to insects that attack all members of the genus they are relatively more abundant. Evidence in support of this may be found in the comparatively large numbers of non-specific insects associated with *Acacia koaia*, a tree that might almost be placed in group 1 and yet is closely allied to the dominant *A. koa*. It is also noteworthy in relation to the main hypothesis that apparently no insects specific to *A. koaia* have evolved.

The results of placing the trees in the abundance groups, and the mean value of specific or unique, "other", and total associated insects for each group will be seen in table 1. It is clear that the more abundant trees have more associated

insects, thus supporting Southwood's (1960) hypothesis. Successive means have been compared by the "t" test and the values for "t" are given in table 1. In the majority of cases these are significant.

As this relationship seems so strong in Hawaii, it is apparent that an important factor in the correlation between the number of associated insect species and tree abundance is evolutionary. What mechanism can we envisage?

The number of insect species that develop resistance to an insecticide is largely determined by the frequency with which different individuals of the insect species are exposed to it. An insecticide that is widely and repeatedly used will have more resistant species than one used locally and irregularly. It is suggested that the evolution of the ability to feed on various trees, which, for example, may involve the production of a mechanism to render non-toxic certain alkaloids or glucosides, or to accept some new chemical as a phagostimulant, is analagous to, although far more complex and slower than the evolution of resistance to insecticides. Insects arriving on the host plant and unable to feed on it must often perish; thus, the number of times individuals of an insect species were exposed to a particular tree would determine whether the tree became a host plant. The number of such encounters would depend on the abundance of the tree and also (although this is not relevant here) on the abundance and the reproductive and dispersal rates of the insect.

Further evidence in support of this view is provided by the observation that when a tree is imported into a new country and grown extensively (e.g. cacao in West Africa) sooner or later several native insects come to feed on it; whereas an introduced tree, without closely allied species in the native flora, that remains relatively rare (e.g. ornamental shrubs such as *Spirea* & *Forsythia* in England) will have few, if any, native insects feeding on it. Furthermore, when a tree becomes more abundant as a result of cultivation, an increasing number of insect species often appear to feed on it. Sometimes this is partly due to transfers from other host plants, as with the mirids *Plesiocoris rugicollis* (Fallen) and *Orthotylus marginalis* Reuter on apple in Britain. In other cases a second type of mechanism seems to come into play in which the increase is due to the invasion of the area by insect species already attached to the host tree in other countries (e.g. with Scot's pine (*Pinus sylvestris*) in southern England since 1930 (Southwood, 1957)). The chances of success of such invasions, especially if we envisage them due to aerial dispersal, will depend on the abundance of the host tree.

It may be objected that the abundance patterns of the trees was largely determined during the Quaternary, but that most insect species had evolved long before this period. This is true, but feeding habits may change quite quickly. For example, the mirids on apple referred to above, the birch feeding Lygaeid, *Kleidocerys resedae* (Panzer), which is now found on *Rhododendron* in southern England, and the two mirids (*Sahlbergella singularis* Hage and *Distantiella theobroma* Distant) on cacao in West Africa (Cotterell, 1930) all appear to have become associated with these new host plants during this century. The cacao

mirids have fed on cacao trees of all ages only in the last fifteen years (Taylor, 1954).

In conclusion, therefore, it is suggested that the relationship between the abundance of a tree and the number of insect species associated with it is primarily an effect of abundance, which determines the number of encounters between an insect species and the tree, thereby influencing the rate of evolution of the ability to feed on that tree. This relationship is further strengthened by the process whereby, when a tree colonises an area outside of its main evolutionary center, its abundance determines the probability of its being found by immigrant individuals of insect species which feed upon it in its original home.

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